Ecological stoichiometry as a foundation for omics-enabled biogeochemical models of soil organic matter decomposition

Emily B. Graham[1,2*] (0000-0002-4623-7076) and Kirsten S. Hofmockel[1,3] (0000-0003-1586-2167)

[1]Earth and Biological Sciences Directorate, Pacific Northwest National Laboratory
[2]School of Biological Sciences, Washington State University, Richland, WA, USA
[3]Department of Agronomy, Iowa State University, Ames, IA, USA

*Corresponding author: emily.graham@pnnl.gov

Abstract.

Coupled biogeochemical cycles drive ecosystem ecology by influencing individual-to-community scale behaviors; yet the development of process-based models that accurately capture these dynamics remains elusive. Soil organic matter (SOM) decomposition in particular is influenced by resource stoichiometry that dictates microbial nutrient acquisition (‘ecological stoichiometry’). Despite its basis in biogeochemical modeling, ecological stoichiometry is only implicitly considered in many high-resolution microbial investigations and the metabolic models they inform. State-of-science SOM decomposition models in both fields have advanced largely separately, but they agree on a need to move beyond pool-based models. This presents an opportunity and a challenge to maximize the strengths of various models across different scales and environmental contexts. To address this challenge, we contend that ecological stoichiometry provides a framework for merging biogeochemical and microbiological models, as both explicitly consider substrate chemistries that are the basis of ecological stoichiometry as applied to SOM decomposition. We highlight two gaps that limit our understanding of SOM decomposition: (1) understanding how individual microorganisms alter metabolic strategies in response to substrate stoichiometry and (2) translating this knowledge to the scale of biogeochemical models. We suggest iterative information exchange to refine the objectives of high-resolution investigations and to specify limited dynamics for representation in large-scale models, resulting in a new class of omics-enabled biogeochemical models. Assimilating theoretical and modelling frameworks from different scientific domains is the next frontier in SOM decomposition modelling, and advancing technologies in the context of stoichiometric theory provides a consistent framework for interpreting molecular data, and further distilling this information into tractable SOM decomposition models.

Key words: carbon use efficiency, carbon cycling, nitrogen cycling, ecosystem models, soil nutrients, microbiome, stoichiometry

Introduction.

The world's soil ecosystems contain a pool of carbon that is larger than vegetation and atmospheric stocks combined, with 1500 Gt C stored in the top one meter alone (Batjes 2016). A large proportion of belowground C is contained in soil organic matter (SOM) whose destabilization has the potential to dramatically alter future climates (Crowther et al. 2019). Soil organic matter decomposition is regulated by physical, chemical, hydrologic, and biological controls (collectively called biophysical controls) on resource availability that determine microbial energy generation and carbon and nutrient acquisition (Robertson et al. 2019; Wang & Houlton 2009; Zhang et al. 2014). These processes are notoriously difficult to measure and predict beyond the scale of experimental plots (Bond-Lamberty et al. 2016; Naylor et al. 2020). Because of this, SOM decomposition at scales most relevant to climate change largely continues to be predicted through generalized environmental proxies such as moisture, temperature, minerology, and total soil C or nutrient pool sizes (Bailey et al. 2018) — parameters that leave a substantial amount of uncertainty surrounding model predictions (Todd-Brown et al. 2014; Todd-Brown et al. 2013). The shortcomings of predicting SOM decomposition beyond localized scales point to a need for scalable spatial and biogeochemical processes in SOM decomposition models (Todd-Brown et al. 2013).

This topic has received considerable attention from multiple scientific domains over the past few decades, resulting in parallel advances between biogeochemical and microbial research (Fig. 1) and calls for greater diversity of measurements used within biogeochemical models (Billings et al. 2021). Collectively, we have made outstanding progress in our understanding of global C cycles; however, a key opportunity remains in integrating theoretical and modelling frameworks from different scientific domains. Existing classes of models each have strengths at different scales and environmental contexts — where one model fails, another excels. Recent work has improved conceptual, empirical, and numerical representations of mineral protection and hydrologic mechanisms that regulate microbial access to SOM (Blankinship et al. 2018; Waring et al. 2020; Woolf & Lehmann 2019). In contrast, detailed representations of the microbial metabolisms that directly convert SOM into carbon dioxide are still missing from predictive models at the ecosystem-scale (Stone et al. 2021). Soil organic matter decomposition (particularly unprotected SOM) is often rate-limited by microbial metabolism (Dwivedi et al. 2019; Hunter et al. 1998; Lehmann & Kleber 2015). In turn, microbial decomposition is coupled to necromass stabilization that is now thought to be the primary mechanism of belowground C storage (Cotrufo et al. 2013; Kallenbach et al. 2015; Kallenbach et al. 2016; Liang et al. 2019; Robertson et al. 2019; Zhang et al. 2021; Fig. 2). Microbial processes and soil physical properties are therefore central considerations in SOM modelling, but they are still coarsely represented in cutting edge SOM decomposition models. Due to recent technological achievements, we now have the ability to measure soil biophysical properties with high molecular resolution (i.e., genes, transcripts, proteins, and metabolites, and soil mineralogy, porosity, chemistry). Our current challenge lies in interpreting and scaling these vast molecular data types into information useful for biogeochemical models (Hall et al. 2018; Malik et al. 2020). Next-generation models that are able to link across molecular to ecosystem scales should enable more robust predictions of SOM decomposition (Chowdhury et al. 2019), with follow-on improvement in global C cycling predictions.

Research Opportunities for Integrating Microbial and Biogeochemical Modelling Approaches

The importance of various controls on decomposition rates differs with the state of SOM at a given point in time and space, the portion of the soil system that is being represented in a given model, and/or with the predictive goal of the model. Biophysical attributes that regulate SOM decomposition collectively vary with soil type and horizon (Patel et al. 2021; Rumpel & Kögel-Knabner 2011); and SOM pool size and composition is dynamic within a single environment. SOM is continuously added to soils through plant litter production, root turnover, and rhizodeposition, while simultaneously being metabolized through microbial decomposition that leads to secondary metabolites and biomass synthesis, all of which have multiple possible routes through soil C cycles (Cotrufo et al. 2013; Liang et al. 2019; Sulman et al. 2014; Wieder et al. 2014). Small changes in the balance of various SOM inputs and subsequent decomposition processes impact the overall fate of C within the Earth system. Embedded in this is an understanding of rate limitation, as soil biology interacts with physiochemistry to constitute a holistic soil ecosystem. In some cases, SOM decomposition may be regulated by abiotic interactions with soil biology — relationships between SOM substrates and microbial decomposition are perhaps most important in the soil organic horizon and within the rhizosphere in mineral layers, where decomposition ultimately regulates C flow to persistent SOM pools

These ideas have been formalized into a biogeochemical model that centers on mineral stabilization while also highlighting the controls of microbial metabolic efficiency on rates of SOM formation and accumulation (Robertson et al. 2019, Fig. 2). While there may be physical limits on the amount of SOM that can accumulate in mineral layers (the C-saturation hypothesis, Six et al. 2002; Stewart et al. 2007), Craig et al. (2021) recently used a simulation model to show that microbial community dynamics which impact biomass C flow are also strong regulators of mineral-stabilized SOM. As such, microorganisms impact SOM cycling across all soil horizons.

Understanding the strength and mechanisms of this regulation across different portions of the soil system (e.g., size fractions and horizons) will further help constrain SOM model development but is beyond the scope of this paper.

Key foci of biogeochemical modelling efforts to improve estimates of SOM decomposition and/or accumulation include mineral-SOM interactions, soil hydrologic properties, chemical speciation of SOM, and microbial bimass and/or microbial use efficiency (Dungait et al. 2012; Robertson et al. 2019; Wieder et al. 2014; Zhang et al. 2021). Physicochemical protection (e.g., mineral-associated ‘MAOM’ or ‘protected pool(s)' vs. 'unprotected pool(s)' including rhizosphere and particulate organic matter) and SOM chemistry in particular are pervasive across most classes of biogeochemical models (Robertson et al. 2019; Sulman et al. 2014; Zhang et al. 2021). For instance, the PROMISE framework centers on SOM accessibility as a key determinant of decomposition, encompassing the known roles of clay mineral composition and heterogeneity in residence times of identical molecules (Müller & Höper 2004; Waring et al. 2020). State-of-science biogeochemical frameworks, even those with an emphasis on physical processes, acknowledge chemical diversity within all SOM pools by using chemical parameters to constrain the fate of various classes SOM and/or generate distribution of decomposition rates for a given pool (Azizi-Rad et al. 2021; Robertson et al. 2019; Waring et al. 2020; Zhang et al. 2021).

While the rate-limiting biophysical factor(s) fluctuates with environmental context, microbial metabolism is the proximate control of bioavailable SOM decomposition in all cases. Because the connectivity between protected and unprotected SOM is already encompassed by state-of-science biogeochemical models, we largely consider processes occurring within unprotected SOM pools when considering avenues for consolidating microbial and biogeochemical models. While we recognize that pore-scale spatial data is critical to understanding SOM decomposition, these data types remain difficult to obtain and are not yet widely used. In contrast, omics data are becoming widespread, and information on microbial communities reflect their underlying physical and chemical habitat. Process-based models arising from microbiology generally represent much smaller spatial and temporal scales than biogeochemical models, with inputs comprised of higher molecular resolution data. They tend to focus on genomic pathways or microbial traits that lead to decompostion (Borer et al. 2019; Borer & Or 2021; Heinken et al. 2021; Malik et al. 2020; Wang & Allison 2021).

Each class of microbial and biogeochemical models provides valuable information on SOM decomposition while also acknowledging considerable error and seeking opportunities for improvement. Therefore, a pressing question remains: how do we merge disperate model structures and underlying theoretical assumptions such that we maximize our predictive power of SOM decomposition, mineralization, and stabilization?

We see a ripe opportunity for harmonizing microbial and biogeochemical SOM models within and across all scales through substrate (plant and microbial) chemistries, which determine SOM composition (from a biogeochemical perspective) as well as the rate and pathway of microbial metabolism (from a microbial perspective). Billings et al. (2021) have identified SOM chemistry as a measurement for the next generation of soil C research, highlighting the increasing usage of molecular advances such as Fourier-Transformed Infrared Spectroscopy (FTIR, Cheng et al. 2006; Keiluweit et al. 2010), mid-infrared spectral libraries (Dangal et al. 2019), and Diffuse Reflectance Fourier-Transformed Infrared (DRIFTS, Kaiser & Ellerbrock 2005; Leue et al. 2010). Substrate chemistry is represented in fine-scale biogeochemical models (e.g., reaction networks and reactive transport models) by influencing reactions with specific

SOM molecules, extracellular enzymes, or inorganic nutrients (Porta et al. 2018; Riley et al. 2014; Wilson et al. 2019). Microbiology also considers substrate chemistry at the individual level (e.g., single cell metabolic models), albeit with different terminology, in the framework of metabolomics. Metabolic models consider substrate chemistry in the context of a model organism's genome to make predictions of growth dynamics or specific metabolomic products (e.g., GEMS, Duarte et al. 2004; Loira et al. 2012; Lu et al. 2019). Biogeochemical models at intermediate scales consider the composition of elemental and SOM pools, often through relatively coarse parameters such as fast vs. slow cycling SOM pools (unprotected vs. protected), mineral SOM, chemical classes or C:N ratios of SOM, and/or organic vs. inorganic nutrient pools. Many recent advances to consider SOM composition have been incorporated in MEND (Wang et al. 2020a; Wang et al. 2015), RESOM (Tang & Riley 2015), CORPSE (Sulman et al. 2014) and MIMICS-CN (Kyker-Snowman et al. 2020), yet none leverage molecular chemical information or stoichiometry of compounds or elements other than C and N. Microbial models at the intermediate-scale simulate interactions between individuals, limited sets of individuals (or as cumulative "mixed-bag" organisms)(Henry et al. 2016), or their characteristic traits to predict metabolite chemistry or changes in the growth of specific organisms or functional guilds (Bouskill et al. 2012; Follows & Dutkiewicz 2011; Malik et al. 2020; Reed et al. 2014). Recent research has also implicitly used the intersection of biogeochemistry and microbiology through substrate chemistry in order to move towards integration by representing fine- (individual microbial metabolisms and metabolites), intermediate- (groups of microorganisms and/or elemental pool composition), and coarse-resolution (multiple interacting microbial groups, "mixed bag" communities, and/or elemental pool sizes) connectivity of microbial drivers and biogeochemical outcomes in predictive models at a particular level of resolution (Fig. 1, 3, 4).

Most of the aforementioned biogeochemical models also include some aspects of mineral-OM interactions and/or soil hydrologic properties.

Despite their coarse representation of microbial processes, biogeochemical models with explicit microbial dynamics represent an improvement over seminal biogeochemical models (Wieder et al. 2013). This has led to soil microbiology research aimed at improving predictions of SOM decomposition through microbial genomics. For instance, Stone et al. (2021) recently demonstrated that the efficiency of microbial SOM decomposition co-varies with taxonomy and soil nutrient status. Other efforts include the prediction of microbial carbon use efficiency from microbial metagenomes (Saifuddin et al. 2019), microbial function under warming (Guo et al. 2020), and SOM decomposition from genome-derived microbial traits (Malik et al. 2020; Wang & Allison 2021) — all of which emerge from decades of work in microbial ecology aiming to understand the role of microbiome composition in SOM decomposition (Graham et al. 2016). State-of-science models in both biogeochemistry and microbiology arise out of a need to move beyond pool-based models towards continuous relationships between microbial metabolism and SOM decomposition and persistence (Tang & Riley 2020; Waring et al. 2020), but they rely on different underlying frameworks such that there are few common concepts, parameters, and equations with which to connect biogeochemical and microbial models.

Ecological stoichiometry (i.e., the role of elemental composition in regulating ecological interactions, Sterner & Elser 2002; Van de Waal et al. 2018) is a useful framework for cross-scale and cross-domain integration. While many biogeochemical models are built on the principles of ecological stoichiometry, they are largely absent from microbial models. Ecological stoichiometry uses the elemental (e.g., C:H:N:O:P:S) imbalance between organisms and their substrates to predict that nutrient limitations universally control biological activity (Elser et al.

2000; Elser et al. 1996; Sterner 1995). It has been leveraged to decipher overarching patterns in the processes governing SOM decomposition (Billings & Ballantyne IV 2013; Sinsabaugh et al. 2013; Sinsabaugh & Shah 2011) and is the guiding framework for decades of biogeochemical investigations that spawned process-based models.

Biogeochemical modelling research has begun to explore the usage of ecological stoichiometry across a broad range of scales. At the largest scale (pool models), a recent update to the CENTURY model (Parton 1996) demonstrates increased accuracy from a tighter coupling of C and N dynamics (Berardi et al. 2020). At higher molecular resolution, Buchkowski et al. (2019) have improved predictions of SOM decomposition by more explicitly accounting for the stoichiometries of microbial biomass and SOM. Fatichi et al. (2019) have proposed direct representation of microbial communities involved in coupled SOM and nutrient cycling, an approach that could not only aid in increasing the accuracy of SOM decomposition predictions but also become a useful tool for empiricists to interpret multidimensional microbial data.

By using an ecological stoichiometry framework to combine new microbiological and computational tools with biogeochemistry, we have an unexploited opportunity to combine predictive models across measurement scales and to better understand global patterns in microbial SOM decomposition. The use of top-down (ecosystem to molecular) and bottom-up (molecular to ecosystem) information exchange guided by ecological stoichiometry can iteratively (1) refine the objectives of high molecular resolution investigations and (2) specify a limited set of dynamics for representation in large-scale models through omics-enabled reaction networks (Fig. 4). Top-down approaches leverage bulk biogeochemical pool sizes to identify nutrient limitation(s) that then guide parameters selection and calibration of reduced complexity models. Bottom-up approaches use stoichiometric principles to guide the analysis and interpretation of large molecular datasets by establishing predictive rules that are translatable across scales. We propose that coupling these methods can specifically improve representations of SOM decomposition within the soil organic layer that ultimately regulate C transport and stabilization in mineral horizons. By using ecological stoichiometry as a conceptual and modelling framework to transfer knowledge across scales and couple existing models, we have the potential to develop a new generation of reduced complexity omics-enabled models.

Ecological Stoichiometry as a Guiding Framework in Soil Organic Matter Decomposition.

Microbial (i.e., fungal, bacterial, archaeal, and viral) degradation of chemically diverse SOM is reliant on broader organismal and soil stoichiometry (Buchkowski et al. 2015; Buchkowski et al. 2019; van Groenigen et al. 2006). Nutrient availabilities in soil determine the metabolic pathways (and their efficiencies) and substrates that are used during SOM decomposition (Ge et al. 2020; Sinsabaugh et al. 2016; Wei et al. 2020). In turn, microbial decomposition and necromass products fuel a cycle of SOM decomposition, formation, and stabilization. Much belowground nitrogen (N) and sulfur (S) is stored within organic matter that is mineralized by soil microbial communities (Freney 1986; Jenkinson 1990; Kirkby et al. 2011). While phosphorus (P) availability is often associated with mineral weathering, the decomposition of organic matter is a key source of P in many ecosystems (Heuck et al. 2015; Margalef et al. 2017). Microbial decomposition increases the bioavailability of plant inputs and SOM by cleaving polymeric compounds into simple C substrates that can be directly assimilated by microorganisms. This process is often catalyzed by extracellular enzymes that release nutrients from organic matter, connecting C, N, S, and P cycling (Allison et al. 2014). Viral predation can also influence these dynamics by lysing specific clades of microorganisms and by influencing organic matter accessibility to microorganisms (Kuzyakov & Mason-Jones 2018; Weinbauer 2004; Wilhelm & Suttle 1999). Global patterns of mechanisms governing SOM formation and cycling and the specific environmental conditions under which certain metabolic pathways are favored by microbial communities are active areas of research.

Identifying parameters that regulate decomposition across different ecosystems is challenging because heterogeneity in nutrient statuses, substrate energetics, mineral and hydrologic properties, and microbial communities can lead to different apparent controls in different soils (Milcu et al. 2011; Sullivan et al. 2014). In some cases, rates of decomposition are linked to microbial adjustments in the acquistion of specific elements in response to differences between microbial biomass and substrate stoichiometries (i.e., nutrient limitations, Billings & Ballantyne IV 2013; Billings & Ziegler 2008; Frost et al. 2005; Manzoni 2017; Manzoni et al. 2008; Spohn 2016; Sterner & Elser 2002). This research is rooted in the paradigm that organisms exhibit stoichiometric homeostasis in which they maintain stable biomass elemental ratios regardless of substrate stoichiometry. It leads to the prediction that nutrient limitations universally regulate biological activity (Redfield 1958; Spohn 2016). Specifically, the relative strength of the relationship between microbial metabolisms involved in N, S, or P acquisition and SOM decomposition should be strongest in soils with the lowest underlying proportion of that element. Indeed, the stoichiometry of microbial biomass features relatively little global variation (60:7:1 C:N:P) (Cleveland & Liptzin 2007) and substrate stoichiometries are highly variable (Frost et al. 2005; Manzoni 2017; Manzoni et al. 2008; Spohn 2016; Sterner & Elser 2002), supporting a dynamic in which microorganisms must adapt to account for soil nutrient concentrations.

The dependency of SOM decomposition on soil nutrients has been investigated most frequently using a suite of biogeochemical techniques in observational or fertilization studies such as CO_2 flux, mass loss, bulk chemistry (e.g., C:N), microbial biomass measurements, and/or potential enzyme activity measurements (Sullivan et al. 2014). Each of these approaches provides indirect evidence for nutrient-regulated microbial decomposition using comparatively low molecular resolution. Additionally, the majority of researchers quanitfy total or coarsely-defined lumped C pools with minimal characterization of specific SOM compound classes or their stoichiometry. For instance, the classical pool and flux model focuses on three or four operationally defined C pools that are connected by biological drivers of decomposition, namely extracellular enzymes (Abramoff et al. 2018). As such, current estimates of nutrient limitations on SOM decomposition vary widely (Cleveland et al. 2006; Grandy et al. 2008; Kirkby et al. 2013; Kirkby et al. 2014; Sullivan et al. 2014; Takriti et al. 2018), and the majority of research has focused on a few elements, generally on linkages between C and N cycling (Cleveland et al. 2006; Grandy et al. 2008; Khan et al. 2016; Kirkby et al. 2013; Kirkby et al. 2014).

Microbial potential enzyme activity remains the primary tool in biogeochemical research for measuring the decomposition potential of specific compound classes in SOM pools. Extracellular enzymes catalyze the depolymerization of complex SOM compounds into simpler molecules for direct uptake and are ubiqutous in soils (Allison et al. 2010). The standard suite of enzyme assays target organic substrates including proteins, carbohydrates, amino sugars, organic phosphates, and lignins (Allison et al. 2007; Burns 1982; Sinsabaugh & Shah 2011). However, several microbially-mediated steps in SOM decomposition—notably those catalyzed by phenol oxidases, peroxidases, and sulfatases which are more constrained by methodological limitations in enzyme activity assays—are under investigated than others (e.g., widely-assayed NAG, BG, phosphatases). Additionally, while the ratios of enzyme activities have been used to assess nutrient limitations (Grandy et al. 2008; Hill et al. 2014; Jing et al. 2020; Moorhead et al. 2013; Sinsabaugh et al. 2008), these assays can be influenced by pH and substrate availability and only provide potential rates. They are low molecular resolution compared to many omics-based apporaches because they target chemical bonds contained by classes of SOM rather than specific molecules, and they can have long turnover times that decouple them from SOM cycling at a specific point in time (Schimel et al. 2017).

Microbial investigations into nutrient-regulated SOM decomposition have traditionally used a complementary set of tools, revealing differences in metabolic strategies to maintain stoichiometric homeostasis using lumped traits (e.g. community-level variation between bacteria and fungi or copiotrophic and oligotrophic metabolisms, Elser et al. 2003; Fierer et al. 2007; Strickland & Rousk 2010). Changes in microbial heterotrophy has also been suggested to vary microbial preferences for C vs. N globally, an inference drawn from primarily biogeochemical data (Taylor & Townsend 2010). Understanding how changes in metabolic strategies of individual microorganisms respond to changes in substrate stoichiometry scale to a microbial community's elemental use efficiency and capacity for decomposition is a key unknown in process-based modelling.

Omics-based characterization of microbial communities (i.e., metagenomic, metatranscriptomic, metaproteomic, and metabolomic) and other high molecular resolution approaches (e.g., chemical probes) provide direct means to evaluate how stoichiometry regulates the ecology of decomposition. These approaches have been highlighted as emerging tools in ecological stoichiometry but are not yet widely implemented (Van de Waal et al. 2018). Microbial genes and their expression patterns can reveal the genetic potential (genes), expression (transcripts), and translation (proteins) of specific enzymes involved in decomposition and more directly evaluate if biological N, S, and P acquisition vary predictably with SOM stoichiometry. While these modern microbial approaches have their own limitations (e.g., data annotation and discrepancies in turnover time when compared to rates), they provide a more complete representation of biogeochemical cycles than enzyme potential assays.

Several potential analysis targets for stoichiometric regulation of SOM decomposition have been identified in omics pipelines. For example, Finn et al. (2020) and Wilhelm et al. (2019) proposed lists of relevant Kyoto Encyclopedia of Genes and Genomes (KEGG) Orthologies and Carbohydrate-Active enzyme database (CAZy) annotations. These contain enzymes involved in the decomposition of organic C as well as N, S, P, and iron cycles, including commonly measured enzymes. They span many classes of enzymes involved in soil C and nutrient cycling, including those targeting cellulose, hemi-celluloses, lignin, cellobiose, mineral and organic N, mineral and organic P, and mineral and organic S. These provide a tangible and comprehensive set of microbial genes, transcripts, proteins, and metabolites that is consistent with biogeochemical methods used to investigate SOM decomposition. New annotations for molecular markers involved in SOM decomposition continue to be discovered, and our ability for molecular resolution into stoichiometry-based processes, if viewed within a consistent framework to biogeochemical applications, can help illuminate patterns where biogeochemical models lack mechanistic resolution.

Opportunities for Ecological Stoichiometry and High-Resolution Measurements in SOM Decomposition Modelling.

Stoichiometric relationships underlie the kinetics of SOM decomposition (for instance, through nutrient limitations) and therefore are essential to developing and incorporating omics-enabled models into ecosystem scale models. The enormous amount of soil microbial and chemical diversity provided by new molecular data types complicates these efforts (Jansson & Hofmockel 2018) such that most current SOM decomposition models cannot yet account for cutting-edge molecular approaches to represent detailed microbial processes. Additionally, there is a need to move beyond models that separate SOM by chemical, physical, and functional properties (e.g., pool-based models) to more fluid relationships between microorganisms and SOM decomposition (Abramoff et al. 2018; Tang & Riley 2020; Waring et al. 2020). Microbial data mining approaches have made incremental advances to this effort, but remaining obstacles underline an opportunity for broader use of ecological frameworks, such as stoichiometric theory, to guide targeted investigations particularly with respect to unprotected pools of SOM (Fig. 2). This approach can help determine which pathways to include in any metabolic model and further scale high molecular resolution predictions to soil ecosystems (Zakem et al. 2020). Below, we highlight opportunities for ecological stoichiometry to inform the development and merging of high-resolution models such as omics-enabled reaction networks with biogeochemical models at larger scales (Fig. 4).

State-of-science models already implicitly use ecological stoichiometry to unify microbiology and biogeochemistry at intermediate scales, as they constrain rates of SOM decomposition with parameters that represent nutrient availability, stoichiometries of organic substrates or microbial biomass, and carbon and nutrient use efficiencies [e.g., MEND (Wang et al. 2020a; Wang et al. 2015), RESOM (Tang & Riley 2015), and MIMICS-CN (Kyker-Snowman et al. 2020)]. These models arise from biogeochemical research and are based on C pools with lumped characteristics. However, they generally include two elements at most, in part due to computational barriers to representing all processes in all elemental cycles as well as their interconnectivity (Abramoff et al. 2018; Moorhead et al. 2012; Sulman et al. 2019; Wang et al. 2015; Wieder et al. 2015).

A small set of coarse parameters is often used to denote microbial processes within state-of-science biogeochemical models, in particular C and nutrient use efficiencies (CUE, NUE) that describe C and nutrient conversion into microbial biomass (Allison et al. 2010; Cleveland & Liptzin 2007; Geyer et al. 2016; Min et al. 2016; Sihi et al. 2016; Sinsabaugh et al. 2013; Sinsabaugh et al. 2016; Wang et al. 2015; Wieder et al. 2014). CUE and NUE incorporate the principles of ecological stoichiometry into microbial-explicit biogeochemical models by serving as proxies for generalized microbial activity. They are most often estimated from empirical measurements of organic matter stoichiometry and/or microbial biomass, or from the ratios of C- vs. nutrient-acquring enzymes (Manzoni et al. 2012; Sinsabaugh et al. 2016). Under nutrient limitation, microorganisms reduce their C uptake, acquire nutrients, and/or respire or excrete excess C as enzymes or metabolites such that C assimilation into biomass often declines (Anderson et al. 2005; Del Giorgio & Cole 1998; Manzoni 2017; Manzoni et al. 2017; Manzoni et al. 2008; Middelboe & Søndergaard 1993; Milcu et al. 2011; Mooshammer et al. 2014b; Smith & Prairie 2004; Sterner & Elser 2002). Thus, CUE typically decreases when nutrients are limiting. In contrast, when nutrients exist in excess, microorganisms adjust their uptake or rate of respiration/excretion to decrease NUE (Milcu et al. 2011; Mooshammer et al. 2014a).

The balance of stoichiometric impacts on decomposition is difficult to predict due in part to microbial interactions (i.e., stoichiometry influences individual behavoir rather than community-level behavoir that ultimately regulates decomposition, Manzoni 2017; Manzoni et al. 2012; Sterner & Elser 2002), highlighting an opportunity for improvement through omics-enabled research. There is also large variation in the relationship of microbial CUE and NUE to SOM decomposition due to spatial and temporal changes in resource availability, microbial community structure, and soil physical properties (Frey et al. 2013; Herron et al. 2009; Malik et al. 2018; Manzoni et al. 2012; Qiao et al. 2019; Sinsabaugh et al. 2013; Sinsabaugh et al. 2016). Biogeochemical models have shown that small changes in CUE can have large impacts on SOM decomposition (Li et al. 2014; Six et al. 2006; Wieder et al. 2013), offering an intriguing possibility for model improvement through detailed representations of nutrient-regulated microbial metabolic pathways to develop scalable omics-enable reaction networks.

At the finest molecular resolution where microbial information is best-suited (Fig. 3), there is a limited set of modelling approaches that currently predict rates of SOM decomposition, largely through by representing genomic and/or metabolic processes. Omics-enabled metabolic models, in particular, infer function from molecular data types by placing annotations within the context of a cell's biochemical abilities to consume substrates, grow, and produce energy (Cuevas et al. 2016). They are capable of including thousands of genes, metabolites, transcriptomes, proteomes, and associated reactions (Lieven et al. 2020; Seaver et al. 2020). However, they are limited by a set of biochemical reactions selected *a priori* that define the possible functions of microorganisms and provide a structure in which to root functional annotations (Seaver et al. 2020). In tandem, flux balance analysis is widely used within omics-enabled models to predict fluxes through the reactions in a metabolic network (Cuevas et al. 2016; Orth et al. 2010). These omics-enabled models can also be coupled to other methods of decoding high-resolution molecular data, such as thermodynamic theory (Garayburu-Caruso et al. 2020; Song et al. 2020), deep learning (Zampieri et al. 2019), or network modelling (Kessell et al. 2020; McClure et al. 2020) to further extend their applicability.

We see opportunity for ecology stoichiometry to provide this framework by guiding representations of microbial metabolism in biogeochemical models, particularly where stoichiometric regulation already exists in the unprotected or biologically-available SOM pools of many microbial-explicit biogeochemical models (e.g., MEND-CN, MIMICS-CN), and as a complement to abiotic controls in mineral soil (Fig. 4). Ecological stoichiometry influences the behavior of individual microorganisms, as they act to maintain stoichiometric balance through adjusting growth rate or biomass stoichiometry and/or mining or excreting nutrients. This understanding could be incorporated into individual-scale models by adjusting active metabolic processes based on environmental nutrient context, for instance through metabolic flux analysis. Increasing in scale towards trait-based models (e.g., Malik et al. 2020; Wang & Allison 2021), ecological stoichiometry operates by impacting the growth rates of organisms with particular traits – for example, microorganisms with specific nutrient acquisition pathways, r- and K- life strategies, stress tolerance, or other competitive advantages. Incorporation of stoichiometric principles such as substrate stoichiometry and/or environmental nutrient status at this scale can guide an individual’s expressed metabolisms in the context of other microorganisms, as well as the interactions of their metabolites and extracellular enzymes, and provides a more computationally favorable model structure. In turn, these omics-enabled representations can provide resolution into SOM cycling that currently aggregates microbial activity via lumped SOM pools and complement existing representations of mineral-sorption processes (Fig. 4).

Ecological stoichiometry can also aid in merging models from microbiology and biogeochemistry by constraining the need for detailed representations of specific SOM decomposition pathways based on environmental context. In a bottom-up approach, ecological stoichiometry provides an overarching hypothesis and sets *a priori* expections for pathways of interest to assist in the interpretation of omics measurements (Fig. 4). Using either hypothesis-driven experiments or observational data from ecological networks, data mining efforts could focus on nutrient acquisition metabolic pathways (e.g., peptidase-, phosphatase-, and sulfatase-including metabolic pathways) in order of hypothesized nutrient limitations in order to compress a multi-omic data set of nearly any size to a manageable amount of data. Data from multiple sources across ecoregions can be leveraged in this way to move towards transferrable principles of SOM decomposition. Metabolic pathways with the most predictive power of SOM decomposition (inferred from transcripts, proteins, and metabolites mapping to metabolic pathways) then guide the portions of intermediate-scale models in which greater resolution of these pathways could lead to more accurate predictions. This could result in inclusion and/or calibration of specific portions of SOM pools that are most tightly coupled to decomposition rates [e.g., protein or necromass pools] or of specific metabolic pathways instead of lower resolution measurements such as CUE and NUE. Dynamically activating omics-enabled reaction networks for a specific nutrient status could provide the maximum benefit of high molecular resolution while being computationally tractable. In turn, parameters and rate estimates made at the intermediate scale can then influence the relative importance of variables in low molecular resolution models such as CUE/NUE, bacterial:fungal biomass, and/or biomass C:N:S:P.

In parallel, top-down approaches use coarsest measurement scale (e.g., bulk biogeochemistry) to first identify nutrient limitation(s) that then guide model development at higher molecular resolutions. Patterns in nutrient concentrations and pool sizes can inform the selection of limited high-resolution parameters for inclusion in reduced complexity models thereby optimizing added value from molecular techniques. For instance, soil nutrient status at a given point in time can be inferred from bulk measurements of soil biogeochemistry and nutrient amendment experiments, and subsequently used to define a set of reactions that should most strongly impact rates of SOM decomposition. Examples might include representing organic N cycles (or amino acid metabolisms therein) for N limitation, microbial biomass recycling (necromass decomposition) for P limitation, and/or organosulfatases for S limitation—or combinations therein in the case of nutrient co-limitation—in omics-enabled reaction networks (Fig. 4). Outcomes from models with enhanced representation of specific SOM decomposition pathways can then further point to specific microbial genes/transcripts/proteins in pathways associated with the rate limiting step in SOM decomposition (if biological). Using this approach, we can narrow down molecular data to specific microbial metabolisms or omics markers of interest to build omics-enabled models including only the most relevant parameters that are scalable to the level of soil ecosystems. This approach reduces the computational cost of high resolution reaction networks by only representing portions of a soil ecosystem that most strongly impact SOM decomposition in detail.

When used in combination, *the result of these iterative approaches is a new suite of models that represent a limited set of microbial metabolisms, guided by stoichiometric principles and high-resolution molecular measurements, that are computationally feasible and more accurately predict SOM decomposition, termed 'omics-enabled biogeochemical models'* (Fig. 4). Such models address a major challenge to the next generation of predictive models—deriving omics-enabled reaction networks that can improve assessments of soil C storage and emissions across molecular-to-ecosystem scales.

Opportunities afforded by investments in new molecular and computational technologies

The power of ecological stoichiometry to guide model development across scales of biological complexity can increase even further when leveraged in combination with new advances in molecular technologies and machine learning algorithms. Research that simultaneously investigates microbial roles in C, N, S, and P cycling is rare, and enzyme activity assays are imprecise relative to omics or probe-based assays. Investments in untargeted molecular approaches are generating new SOM cycling analyses by allowing detection of active microbial metabolisms. These are nascent technologies that have the potential to improve our understanding of SOM decomposition but need greater usage and development to surmount remaining challenges.

We especially highlight stable isotope probing (SIP, Bernard et al. 2007; Dumont & Murrell 2005; Pepe-Ranney et al. 2016), new ultrahigh-resolution metabolomics (Tfaily et al. 2017), activity-based protein profiling (ABPP, Killinger et al. 2019), and machine learning as new classes of technologies deserving of further development and broader consideration. Briefly, microbial applications of SIP use substrates enriched in heavy isotopes (e.g., ^{13}C, ^{18}O, ^{15}N) amended to microbial communities to reveal isotope-labeled biomarkers of active microbial populations (Bernard et al. 2007; Dumont & Murrell 2005; Pepe-Ranney et al. 2016). While SIP has long been used in biogeochemistry, recent advances are increasing the tractability of SIP within amplicon profiles, metagenomes, metatranscriptomes, and metaproteomes (Barnett & Buckley 2020; Jameson et al. 2017; Pepe-Ranney et al. 2016; Wilhelm et al. 2019; Youngblut et al. 2018a; Youngblut et al. 2018b). In parallelel, ultrahigh-resolution metabolomics, such as Fourier transform ion cyclotron resonance mass spectrometry (FTICR-MS, Tfaily et al. 2015; Tfaily et al. 2017), can illuminate new aspects of SOM chemistry by enabling the determination of elemental stoichiometry in thousands of SOM molecules simultaneously (Tfaily et al. 2017). Formulas assigned via ultrahigh-resolution metabolomics are a promising tool for evaluating metabolisms influenced by ecological stoichiometry by providing information on molecules with specific stoichiometries (e.g., C:N ratios of SOM molecules in a standing pool) or changes in these molecules during the course of experiments. Finally, new targeted approaches can improve the accuracy of existing enzyme-based approaches. Activity-based protein profiling (ABPP, Killinger et al. 2019), for example, leverages chemical probes that react irreversibly with protein families to identify enzymes binding to specific molecules, and when paired with mass spectrometry-based approaches, can also quantify rates of enzyme production (Killinger et al. 2019). In contrast to enzyme activity assays that reveal potential enzyme rates, ABPP has the potential to dramatically improve investigations of SOM decomposition by revealing the true expression of decomposition enzymes; however, it has never been used in soils (Sadler & Wright 2015; Whidbey & Wright 2018; Zegeye et al. 2020).

Even with technological advances, the interpretation of untargeted molecular approaches is complicated by the inadequate description of metabolic pathways for soil microorganisms in existing databases and the unsuitability of standard statistical approaches in ecology for combining multidimensional data types. Unsupervised machine learning is emerging as a tool both to decipher hidden patterns in complex data and to eliminate the needs for *a priori* relationships between genes (e.g., via metabolic pathways or metagenome-assembled genomes) and for gap filling to infer absent data. There is an enormous diversity of machine learning algorithms with varying levels of complexity that are well-suited to discern patterns in data (Rana et al. 2020; Were et al. 2015). Techniques such as K-nearest-neighbor (Peterson 2009), artificial neural network (ANN, Sarle 1994), support vector machines (SVM, Wang 2005), neuro-fuzzy (Nauck et al. 1997), decision tree classifiers (Safavian & Landgrebe 1991), and random forests (Liaw & Wiener 2002) are most commonly employed in microbiology and environmental disciplines (e.g., Cai et al. 2019; De Clercq et al. 2019; Dong & Chen 2019; Qdais et al. 2010; Rahimian Boogar et al. 2019; Thompson et al. 2019; Wang et al. 2020b). Still, we lack rigorous machine learning investigations in which sampling and experimental designs move beyond feature identification to translating selected features into meaningful ecological outcomes. Pairing machine learning with ecological theory for experimental hypothesis testing is needed to push fundamental biology forward (Rana et al. 2020; Were et al. 2015). Using new high-resolution molecular data types in spatially- and temporally-distributed sampling, paired with machine learning, is the gold standard for future research in SOM decomposition and can offer unprecedented untargeted resolution into the pathways by which microorganisms decompose SOM (Manzoni et al. 2017; Mooshammer et al. 2014b).

Conclusions.

We have made significant advances in understanding global C cycles and now face the challenge of merging concepts and modelling frameworks from different scientific fields. To facilitate this effort, we identify substrate chemistry as a linkage point between microbiology and biogeochemistry, and we propose using ecological stoichiometry as a unifying framework that can help overcome a major limtation to understanding global SOM decomposition — intrepreting the massive amount of data generated by molecular approaches and translating them to the ecosystem scale. Our hope is that this common foundation can maximize the strengths of models across scales and environmental contexts, and we encourage better communication among empiricists and modelers within and across domains. Investing in and deploying new technologies in the context of stoichiometric theory provides an untapped and promising avenue for interpreting the vast amount of data we can now generate and further distilling this information into a new generation of omics-enabled biogeochemical models.

Acknowledgements. We thank Hyun-Seob Song and two anonymous reviewers for helpful comments on this manuscript. This research was supported by the US Department of Energy Office of Biological and Environmental Research (BER) and is a contribution to the Scientific Focus Area ‘Phenotypic response of the soil microbiome to environmental perturbations’. Pacific Northwest National Laboratory is operated for the Department of Energy by Battelle Memorial Institute under contract DE-AC05-76RLO1830.

Declarations.

Funding. This research was supported by the US Department of Energy Office of Biological and Environmental Research (BER) and is a contribution to the Scientific Focus Area ‘Phenotypic response of the soil microbiome to environmental perturbations’. Pacific Northwest National Laboratory is operated for the Department of Energy by Battelle Memorial Institute under contract DE-AC05-76RLO1830.

Conflicts of interest/Competing interests. We declare no conflicts of interest/competing interests.

Availability of data and material (data transparency). Not applicable.

Code availability (software application or custom code). Not applicable.

Authors' contributions. EBG conceived and wrote the manuscript with significant contributions from KSH.

Figures.

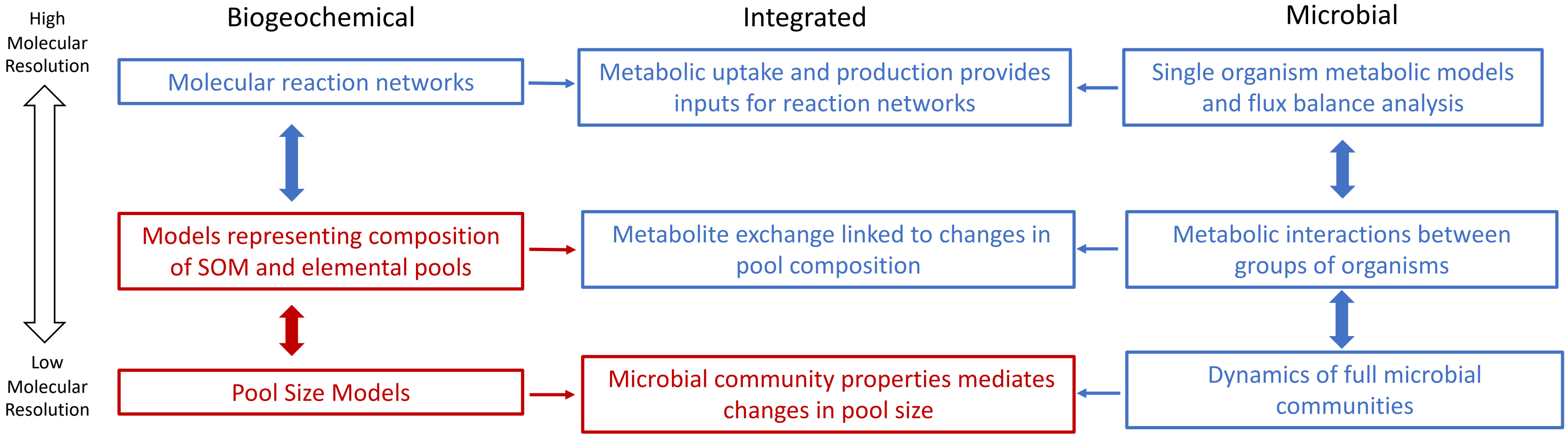
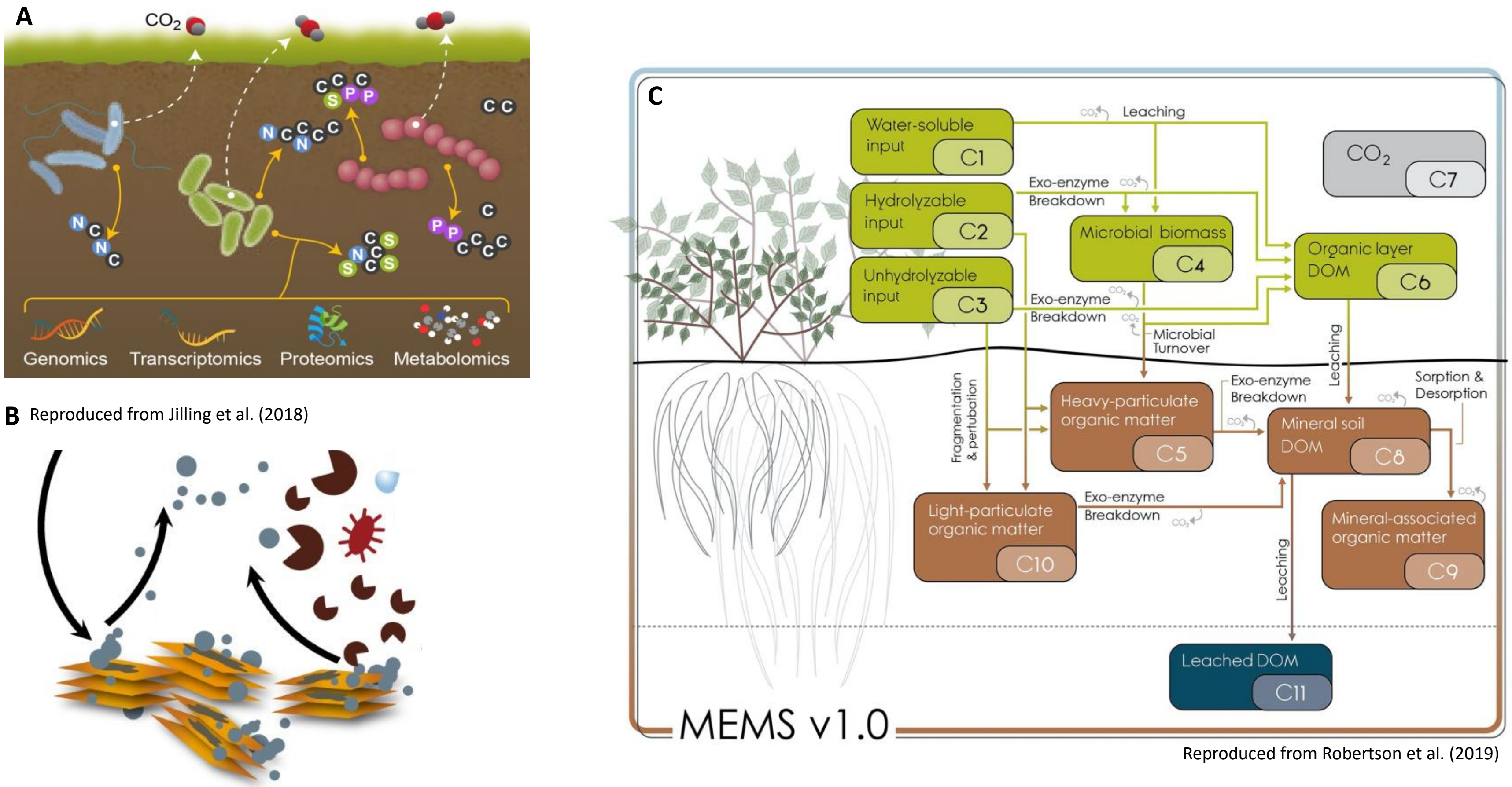


Fig 2. Parallel development of processed-based biogeochemical and microbial models across scales of molecular resolution. A short description of a representative class of models from biogeochemical (left) vs. microbiological (right) research domains is listed within each box. Model types that bridge between microbial and biogeochemical research domains are in the center column. High molecular resolution models are on the top row and low molecular resolution models are on the bottom row. Modelling frameworks that leverage ecological stoichiometry are depicted in red, and opportunities to use these principles to guide multiscale model development are depicted in blue. We present opportunities for stoichiometry to serve as an underlying framework to integrate state-of-science SOM decomposition models across ecological hierarchies – from individual microorganisms to bulk pools and fluxes – as well biogeochemical and microbial disciplines. Ecological stoichiometry is implicitly used to guide both biogeochemical and microbiological models and therefore presents a natural linkage point for assimilating and scaling models from both research domains.



Reproduced from Jilling et al. (2018)

Reproduced from Robertson et al. (2019)

Fig. 2. Overview of Factors Regulating Soil Carbon Cycles. (A) Microbial metabolism is the proximate control over bioavailable C cycling. These controls dominate in unprotected SOM pools in which accessibility is not limited and provide an avenue for stoichiometry to improve model predictions. (B) Mineral-association and hydrologic variables are also key components of SOM

cycling, particularly in deeper soil horizons with high mineral content. (C) These conceptualizations are consolidated within the MEMS framework. In MEMS, SOM is more readily bioavailable in the organic horizon where growth of microbial biomass and to a lesser extent dissolved organic matter support C flow to and stabilization within mineral horizons. Panels (B) and (C) are reproduced from Jilling et al. (2018) and Robertson et al. (2019).

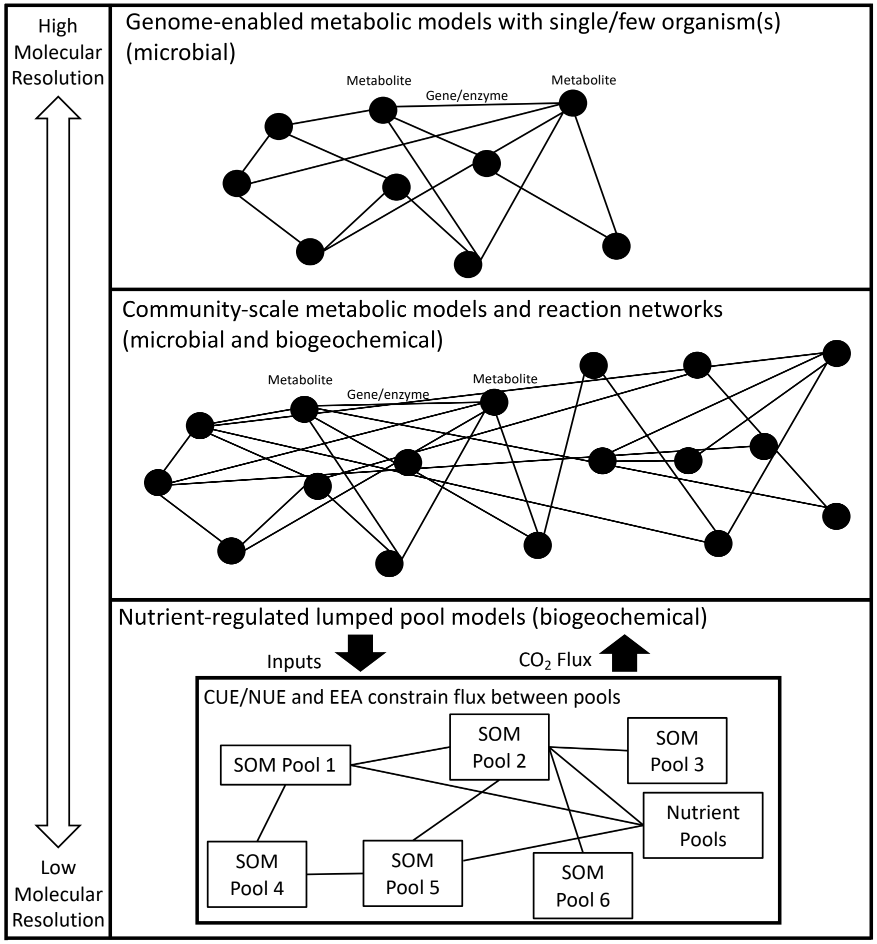


Fig 3. Representation of state-of-science SOM decomposition models across scales of molecular resolution. At the highest level of molecular resolution (top), genome-enabled models predict the production and consumption of specific metabolites by specific microorganisms or groups of microorganisms. This class of models is rooted in fundamental microbiology. At intermediate scales,

community-scale (mixed-bag) metabolic models and reaction networks have been largely separately developed in microbiology and biogeochemistry, respectively. Finally, at coarser levels of molecular resolution, biogeochemical models predict SOM decomposition using nutrient-regulated exchange between lumped SOM pools with specific chemical attributes.

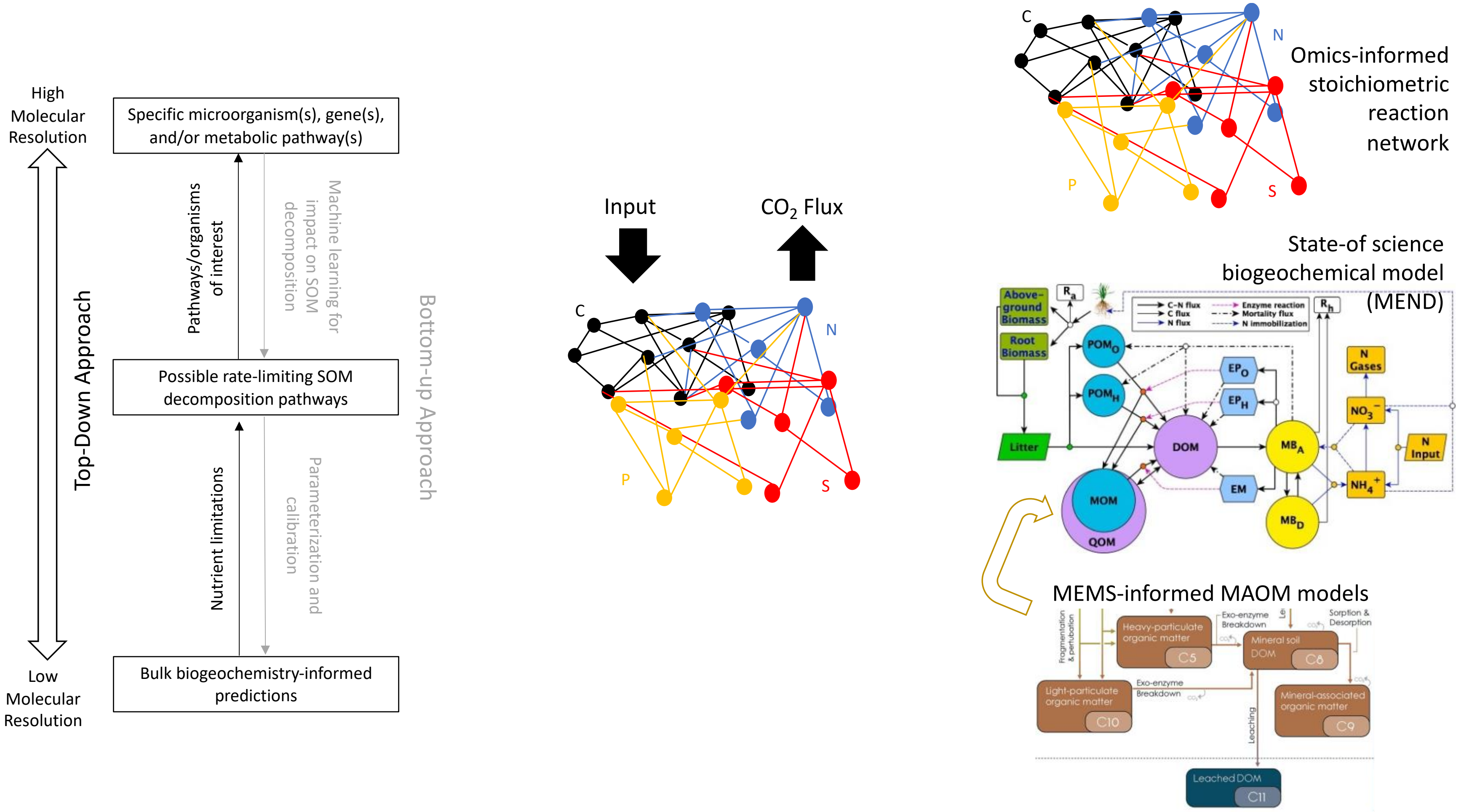


Fig 4. Schematic of opportunities for ecological stoichiometry to guide iterative approaches that generate omics-enabled biogeochemical models. Ecological stoichiometry can guide a cycle of top-down and bottom-up approaches for more efficient generation of next generation models. Top-down approaches use nutrient limitations inferred from bulk biogeochemical measurements

to guide the determination of rate-limiting pathways in SOM decomposition. In turn, rate-limiting pathways can reveal specific metabolic pathways and/or microorganism for detailed representation in predictive models. Bottom-up approaches use ecological stoichiometry as a framework for guiding the interpretation of high molecular resolution data streams with the help of new machine learning algorithms, for example by focusing on metabolic pathways that tend to be involved in nutrient acquisition. Using these approaches to identify the rate-limiting steps of SOM decomposition can then aid in the parameterization and calibration of larger-scale models by informing the tuning of substrate use efficiencies and/or by revealing pathways for more detailed representation. By using both approaches iteratively, we can identify specific portions of genome-enabled reaction networks that add predictive power with detailed representation in large-scale SOM decomposition models. A schematic of iterative top-down and bottom-up approaches is shown on the left. This leads to the development of a stoichiometry-informed reaction networks (middle) that can be merged into existing state-of-science SOM decomposition models (right).

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